THE TYPE SPECIES OF THREE UPPER PALAEOZOIC PUNCTATE SPIRIFEROIDS

by K. S. W. CAMPBELL

ABSTRACT. The type species of *Spiriferellina* Fredericks, *Reticulariina* Fredericks and *Punctospirifer* North are redescribed from type material.

INTRODUCTION

To date eight genera of Upper Palaeozoic punctate spirifers have been erected. Two of them, *Crenispirifer* Stehli 1954 and *Altiplectus* Stehli 1954, are well known from modern work. Interpretations of the other genera are many, but all lack authority because of inadequate knowledge of the type species.

In the case of *Paraspiriferina* Reed, erected as a subgenus of *Spiriferina* to embrace *S. multiplicata punjabensis* Reed and *S.* (*Paraspiriferina*) *ghundiensis* Reed, and *Callispirina* Cooper and Muir-Wood (type species *Spiriferina ornata* Waagen), the original diagnosis and descriptions are concerned only with the general form of the shell, and the arrangement and number of the plicae. Information on the surface ornament and interior is either completely lacking or is very vague. The type species come from the Salt Range. The genera remain virtually uninterpretable.

The genus *Spiriferinaella* Fredericks (type species *Spiriferina artiensis* Stuckenberg) is very poorly known, but it is unlikely to be confused with any of the other genera because of its very transverse outline, few low plicae, denticulate hinge, and deep denticle grooves on the pedicle cardinal area.

Reticulariina Fredericks 1916 (type species *Spiriferina spinosa* Norwood and Pratten, from the Mississippian Chester Series of Illinois) has been relatively well known from the work of Hall and Clarke (1893) and Weller (1914). It is easily distinguished from the other described genera by the large hollow spines scattered over the surface. Difficulties have recently arisen, however, in that several species of Permian age from South America and India (Chronic 1953; Reed 1944) have been assigned to the genus primarily on the basis of the presence of coarse spines, without adequate comparison of other features.

The two genera most often confused in the literature are *Spiriferellina* Fredericks 1919 (type species *Terebratulites cristatus* Schlotheim from the Zechstein of Germany) and *Punctospirifer* North 1920 (type species *Punctospirifer scabricosta* North from the Viséan of England). Neither of the authors concerned appears to have been aware of the work of the other, and their papers were published at almost the same time. The early revisers of the group concluded that there was an overlap between the two genera as they were originally defined, such, for example, as was pithily expressed by Paeckelmann's '*Punctospirifer*+paläozoische Formen von *Spiriferina* s. str. North sind = *Spiriferellina* Fred . . .'. Muir-Wood (1948, pp. 63–64) concluded that *Punctospirifer* may be distinguished from *Spiriferellina* 'in having more numerous and less angular plications on the lateral slopes, and in having a more flattened, broader median fold, and shallower

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sinus. In *Spiriferellina* the cardinal area is not sharply demarcated from the lateral slopes. The concentric lamellose ornament is more prominent in *Punctospirifer*. There are also considerable differences in the internal structure of the two genera.' As will be seen from this, the differences consist entirely in the relative degree of development of certain characters, except perhaps in the case of the internal differences, the nature of which have never been made explicit.

The present work has been concerned with the redescription of the type species of *Spiriferellina*, *Reticulariina*, and *Punctospirifer*. In the case of *Spiriferellina cristata* I have been able to examine the syntypes, as well as several specimens from the same horizon as the syntypes at Pössneck. The holotype, paratypes, and numerous topotypes of *Punctospirifer scabricosta*, and several topotypes of *Reticulariina spinosa* as well as other specimens from the Chester Series at Paint Creek, have been examined.

I have not been concerned with the definition of genera as such, but only with the type species, and in this way I have hoped to provide a basis for wider discussion.

Punctospirifer scabricosta North

Plate 58, figs. 1–10; Plate 60, figs. 1, 2

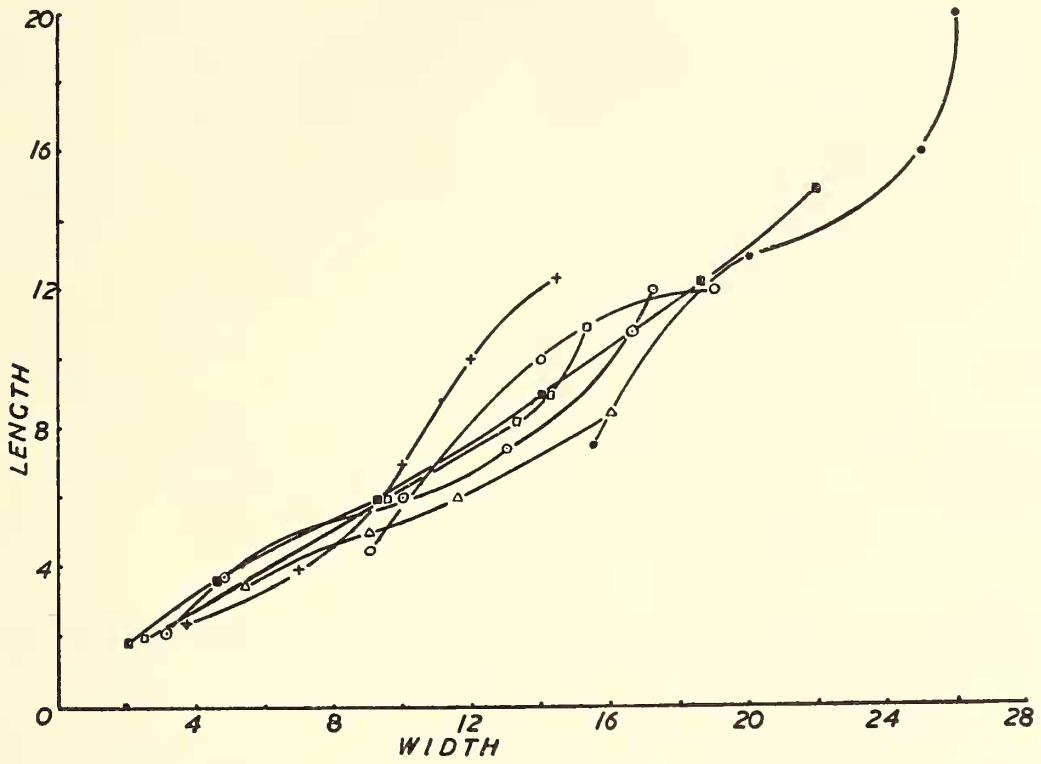
Material. Holotype 64285 G.S.M. from Viséan, Ashfell Edge, Westmorland, England. About twenty topotypes G.S.M., and about fifty topotypes S.M.

Description. The shell at the adult stage is transverse, with sub-rectangular to moderately acute or even faintly mucronate cardinal extremities. At the earliest stages (up to *c.* 5 mm. in width) the extremities are slightly rounded, following which they gradually become angular and then slightly mucronate. This stage may persist through to the adult, or as is more common, the mucros are gradually reduced and sub-rectangular extremities are produced. The pedicle cardinal area is high, the distance between the tips of the two umbones reaching as much as half of the total shell length. In most cases this area is concave immediately beneath the umbo, but flattens out towards the hinge, where it lies almost at right angles to the plane of the commissure. In some specimens, however, the relative rates of deposition on the hinge and commissure remains constant throughout growth so that the area is more or less planar. This combination of high cardinal area and extended hinge line throughout all but the earliest growth stages produces the prominent, sharp, cardinal ridges so often regarded as diagnostic of *Punctospirifer*. The cardinal ridges, of course, are merely the loci of the cardinal extremities during growth. The surface of the cardinal area carries growth lines, often crossed at right angles by very weak lineations. There is no indication, however, of denticle grooves.

The delthyrium is quite uncovered and is bordered by the prominent dental flanges which are at a slightly lower level than that of the cardinal area. The delthyrial angle averages 29° (range 25° to 32° for six specimens). The sinus is deep and V-shaped in transverse section, and often there is a weak median furrow in it. The sinal angle averages 27° (range 23° to 32° for six specimens). There are usually eight or nine well-rounded and regularly spaced plicae on each of the lateral slopes in adults.

The brachial valve is only moderately convex in anterior profile and is almost flat along the crest of the fold in lateral profile. The fold is prominent with steep sides and rounded crest, while the form of the plication in the commissure is high and either well rounded or more commonly sub-ogival.

The whole outer surface of the shell, apart from the cardinal areas, is covered with fine, closely spaced imbricating lamellae. There are, of course, irregularities of growth shown on the surface as accentuated aggregates of growth lamellae, but taken by and large the general impression is one of regularity and close spacing. Crossing the lamellae is a series of very fine radial threads which are often in line on adjacent lamellae, so that they could well be called radial lirae. They number 15 to 22 per mm., and are similarly



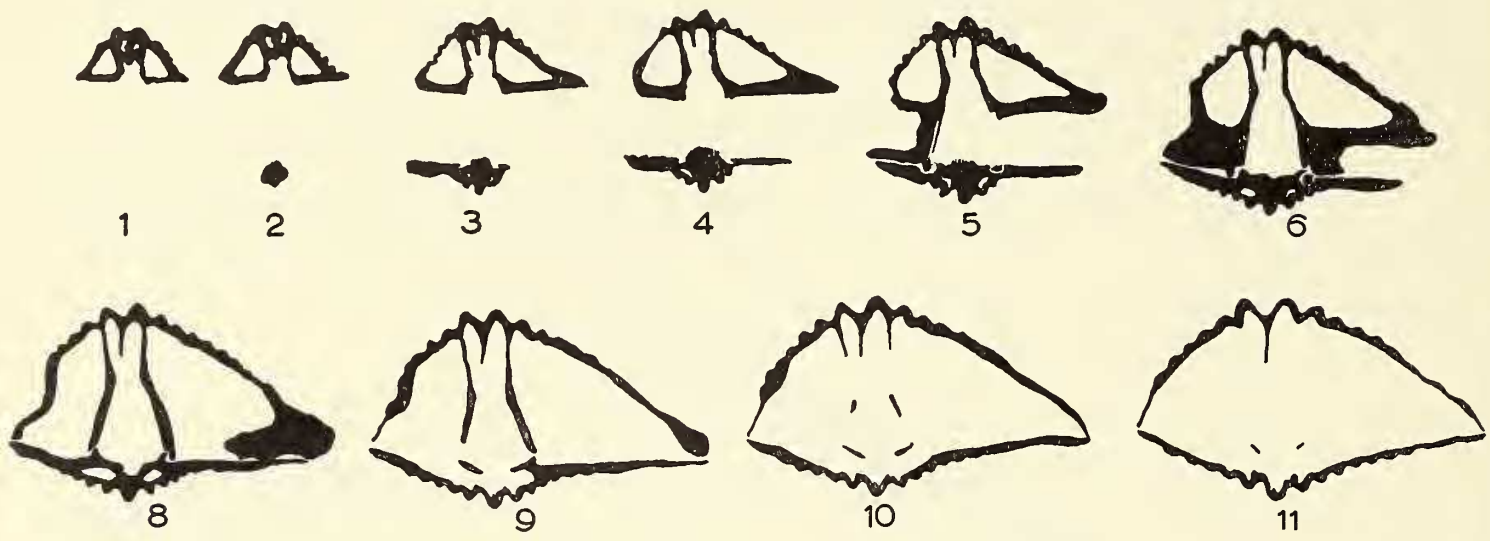
TEXT-FIG. 1. Plot of length/width (in mm.) of pedicle valves of *P. scabricosta* to show the variation during individual ontogenies.

spaced over the whole surface. On the posterior portions of some specimens they seem to be slightly raised into extremely minute projections, causing an almost imperceptible serration of the lamellar edge. This, however, is very rare. No sign of spines or spine bases has been observed. In the bottom of the sinus and inter-plical depressions the lirae are truly radial but they fan out up the sides. The crests of the plicae are invariably worn and the lirae are obliterated.

Interior. The dental lamellae are low, reaching a maximum depth of about one-third the distance from the umbo to the tooth, and gradually taper from that point to the hinge. Along their inner face there is usually a rather sharp flange. They are quite thick in comparison with the adminicula which extend *c*. one-third of the length of the valve along the floor from the umbo. They invariably run down the furrow between the first and second plicae from the sinus. The median septum runs approximately half the length of the valve. It originates in the umbo in a very small, slightly elongate callus of variable size, and increases gradually in size to its sharp antero-dorsal tip where it is slightly undercut and drops away in a sharp curve to the shell wall. In some specimens its junction with the floor of the valve is quite angular while in others it is a smooth curve. The arrangement of the muscle scars has not been determined. In section, however, it is seen that secondary deposition took place well up the sides of the median septum and there

is often an abrupt break at the dorsal edge of this deposition. It is probable that this secondary material was laid down on the site of adductor attachment (see text-figs. 2, 3).

The umbo of the brachial valve is solid. The sockets appear to be rather shallow until the adult stage is reached when they broaden out and become bulbous. In some specimens they encroach on the crural plates. The socket plates arise as strong rounded ridges from the wall of the shell, and they fade out laterally in front of the hinge. The crural plates are welded into the umbonal complex and are not supported on adminicula.

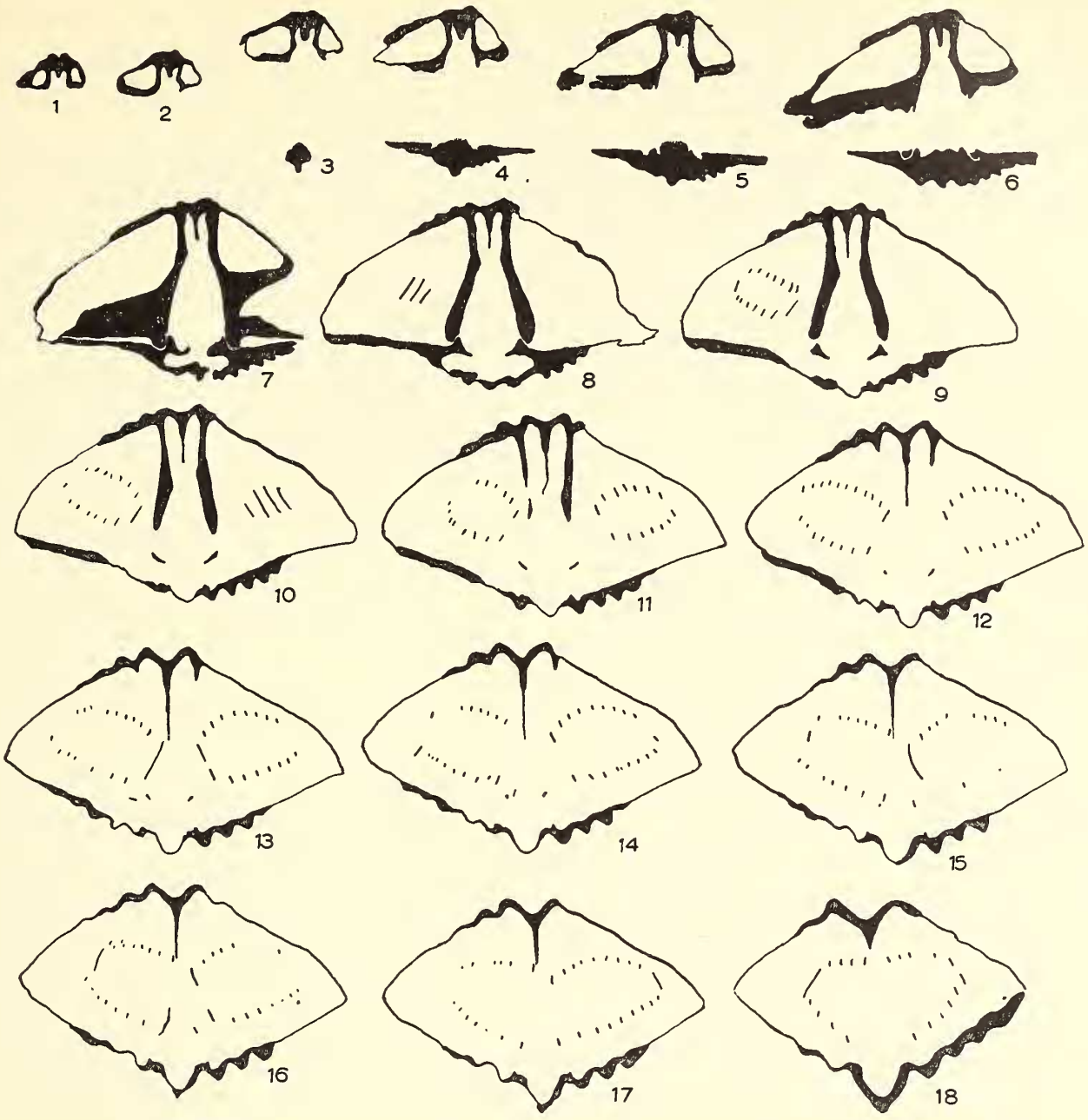


TEXT-FIG. 2. Serial sections of a specimen of *Punctospirifer scabricosta* North. The interval between sections 9 and 10 is 0·02 inch; the remainder are 0·01 inch. ×2. BB. 20431, B.M.

Their inner faces are strongly concave. Arising between the crural plates is a broad cardinal process. The postero-dorsal edges of the crural plates give the impression of being tucked in behind the cardinal process. The anterior face of the cardinal process is smooth towards the base, but ventrally it begins to become furrowed and its postero-ventral face is deeply divided into about twenty platelets. Encroaching on to the base of the cardinal process and the inner edges of the crural plates there may be a layer of shell tissue connected with the outer wall. The crural plates and process themselves are formed of impunctate tissue and this investing material can be easily detected since it is punctate.

Dividing the muscle field is a very weak median ridge which is continuous into the umbonal thickening. The central pair of adductors are very long. In adults they have their posterior edge *c.* 2·5 to 3 mm. forward of the umbo. They vary considerably in length and in width. In one of the three specimens where they are well exposed they reach a length of 6 mm. (total length of valve 11 mm.) though in the other two they are relatively shorter—4·5 mm. and 5 mm. in total lengths of 11 mm. each. The central scars spread out on to the furrows bordering the fold and even, occasionally, encroach on the first lateral plica. Posteriorly they are slightly depressed, and laterally they are bounded by clear-cut ridges which fade away almost completely to the front. These lateral bounding ridges extend backwards almost to the crural plates as bases for the attachment of the outer edges of the postero-lateral adductors.

The spires are directed postero-laterally and in adults there are *c.* twelve volutions in each spire. In none of the five specimens I have sectioned is there any sign of a jugum, and since the spires in two of these specimens are still more or less in position, I believe



TEXT-FIG. 3. Serial sections of a specimen of *Punctospirifer scabricosta* North. The intervals between sections 1 and 2, and 7 to 13, are 0·02 inch; between 17 and 18 it is 0·06 inch; the remainder are 0·01 inch. ×1½. 64284 Garwood Collection, G.S.M.

that, at least in these, a jugum was never present. There do not appear to be any spines on the spires.

Remarks. North gives the number of plicae on the lateral slopes as seven to ten, but almost every specimen I have examined has either eight or nine. The structure of the jugum remains a problem. North (p. 213) records that it is 'slender, and forms a shallow V-shaped process, with its apex directed ventrally and posteriorly'. Stehli (1954) states that this is probably erroneous and that the jugum in certain specimens he has examined is anteriorly directed, but he does not make it clear whether or not his observations are on topotypes. My own observations indicate that the jugum was not always developed.

The fine radial ornament on the holotype appears to be less regularly developed than in the figured topotype, and the radial threads are not continuous from lamella to lamella but rather increase in size on each lamella from back to front. Well-preserved specimens always show the arrangement of the figured topotype, and there is little doubt that the condition of the holotype is due to slight wear.

Reticulariina spinosa (Norwood and Pratten)

Plate 59, figs. 10–14; Plate 60, figs. 4, 5

Material. Five specimens in the Davidson Collection at the British Museum, from the Mississippian Chester Limestone, Chester, Illinois, and bearing a label 'given to me by Mr. Worthen'. Twenty-five specimens from the Illinois Geol. Surv. Coll., also collected by Amos Worthen, from the same locality.

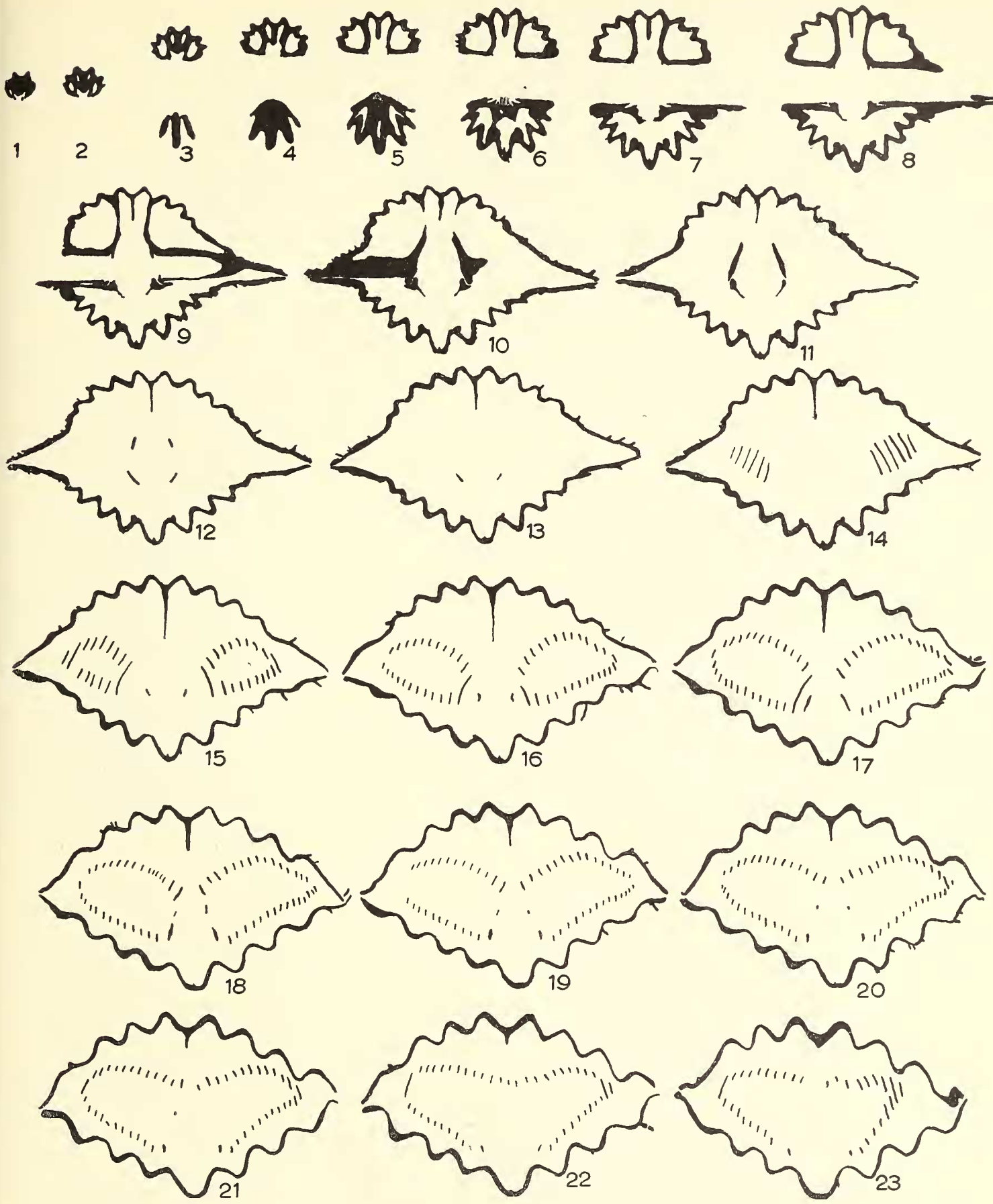
Description. This species reaches a large size for a Palaeozoic punctate spirifer. The outline is invariably transverse, the length being about three-fifths of the width.

The cardinal area of the pedicle valve is low and rather strongly concave, and the umbo does not project far behind the hinge. The delthyrial angle averages 45°. At all stages of ontogeny the cardinal extremities are rounded, except in an occasional specimen in which they tend to be sub-rectangular or even slightly acute. There is no evidence that the shape of the extremities changes during ontogeny. The sinus is usually well rounded and the sinal angle averages 22°. There are five plicae on each of the lateral slopes, and occasional traces of a sixth. In section the plicae tend to be flat sided and well rounded on the crest.

In lateral profile the brachial valve is highly arched. The fold is well rounded overall, but carries a very faint median depression in most specimens.

The superficial shell layer is very thin and shows extremely fine growth lines, spaced *c.* 15–20 per mm. There is no sign of lamellation or imbrication such as occurs in the other punctate genera, but only occasional growth halts which become more numerous toward the front of the shell. The surface also carries a large number of tubular spines which reach a far greater size than those of any other described punctate spirifer. In general the spines are largest on the crests of the plicae and decrease in size on their flanks. They are generally absent from the base of the inter-plical furrows, though occasionally an isolated one is found. On the axial region of the sinus the spines are enlarged. Towards the umbo they are arranged in a single irregular zigzag row, but towards the front they have no clear-cut pattern. On the brachial valve the pattern of spine arrangement is similar to that of the pedicle, except that large spines of the same size as those on the crests of the plicae occur on the crest of the fold, while those on its flanks are of a lesser size. All spines are set at a low angle to the shell surface and are radially disposed with respect to the umbo. Because of this, they leave an elliptical scar where they break off. Scars with a long axis of 0·4 mm. are not uncommon, while the smaller ones are often down to 0·1 mm. In external diameter the spines are up to 0·3 mm. at their base, but most are smaller. They taper very gradually. Their length is not definitely known, but fragments up to 1·5 mm. have been observed. They seem to be formed from the outer shell layer, the inner one being extremely thin, if it is present at all. The spines were occupied by mantle tissue only whilst they were at the growing edge. Subsequently they were sealed off by the normal punctate secondary shell layer.

The cardinal area of the pedicle valve is subdivided into broad, almost smooth, portions on either side of the delthyrium and narrow subtriangular spine-bearing portions against the cardinal ridges. There is a sharp, slightly raised line of division between the two regions. The inner portions are smooth except for faint growth lines and weak, irregular transverse striae. These latter are not denticle grooves—denticles are never developed. The spines on the outer portions show no clear-cut pattern. They are



TEXT-FIG. 4. Serial sections of a specimen of *Reticulariina spinosa* (Norwood and Pratten). The intervals between sections 14 to 17, and 22 to 23, are all 0·02 inch; the remainder are 0·01 inch. ×2. S 16225, S.M.

rather smaller than the average for spines on the body of the shell and are set at a high angle to the surface of the cardinal area. Their average diameter at their base is 0·1 mm. with a range of 0·05 to 0·15 mm. The cardinal area of the brachial valve is similarly subdivided, though the spinose region is so narrow that it is imperceptible on most specimens.

The punctae of the secondary layer either stop short at the primary layer, or they just penetrate its base. So far as I am able to determine, wherever the primary layer is undisturbed the punctae fail to reach the surface of the shell. Their diameter is 0·06 to 0·1 mm., most being approximately 0·075 mm., and they are spaced 75 to 100 per sq. mm. On the cardinal area they are somewhat finer and slightly more closely spaced.

Interior. The callus in the tip of the umbo is very small and results in the septum being united with the inner faces of the adminicula. The septum is as shown in text-fig. 6. It is a slender structure with secondary deposition on its sides as in *P. scabricosta*, and it reaches approximately half the length of the shell. The dental lamellae and adminicula are moderately thick, the latter reaching about one-third the length of the shell and run along the furrows immediately lateral to the sinus. The diductor insertions are not known.

The cardinal process is a small recessive structure situated on a very low umbonal callus. The crural plates are broad and concave on their inner faces with their inner edges sharply inflected. The descending lamellae are straight and sub-parallel to the jugum, but forward from that structure they diverge and swing away dorsally. The jugum, in the only specimen in which it has been observed, consists of a pair of prongs directed antero-ventrally and slightly inwards toward the median plane. They do not appear to meet. There are *c.* sixteen volutions in the spires of adults. A weak median keel divides the adductor scars which reach *c.* half the length of the valve. The ridges on the outer edges of the postero-lateral adductor scars are strong, rounded, and rise abruptly from the shell wall. They are situated on the outer side of the crest of the furrow bordering the fold.

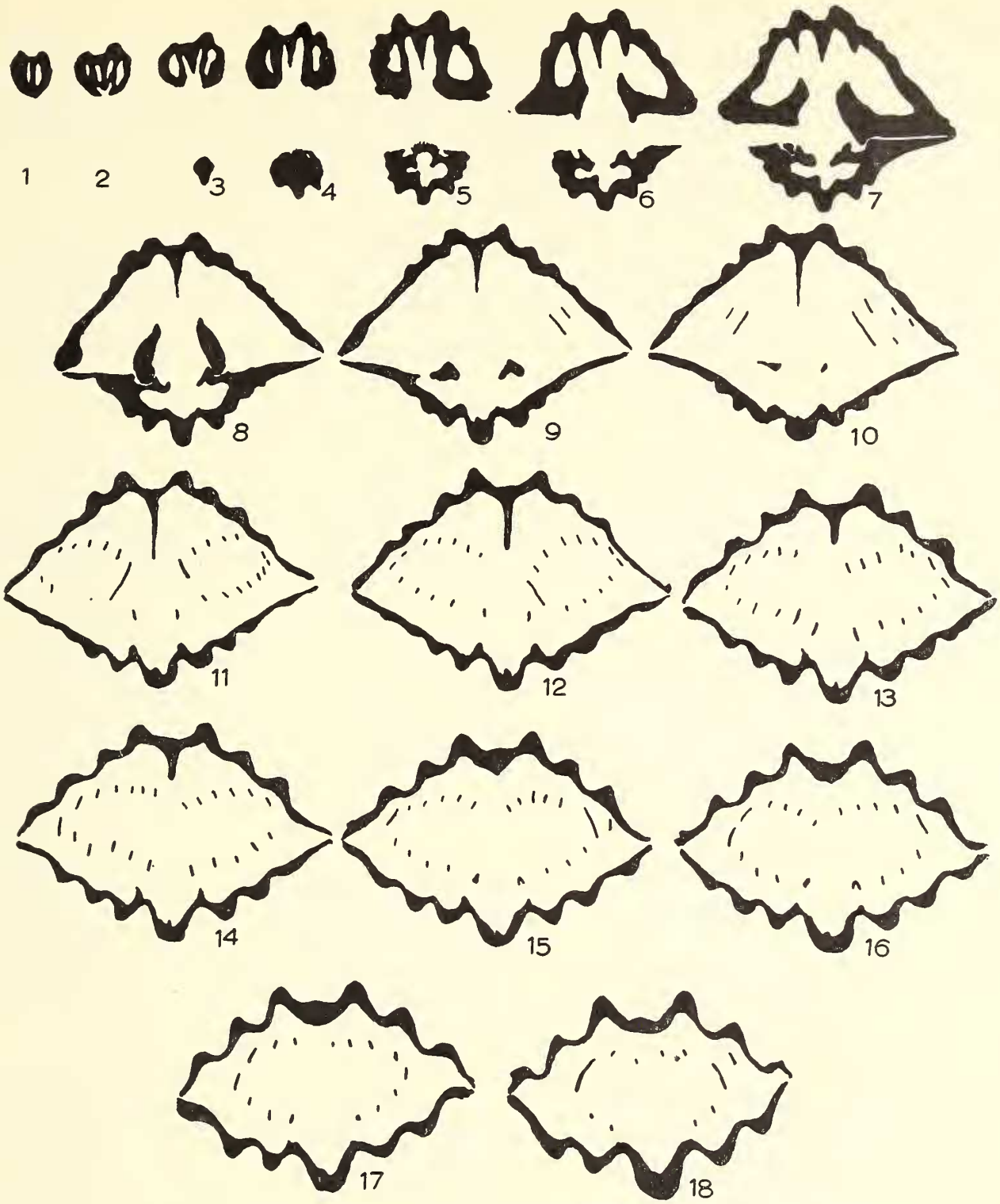
Remarks. This description differs from the original of Norwood and Pratten in a number of points. The growth lines (striae of N. and P.) are not imbricate except towards the front of occasional specimens; the spines are never at right angles to the shell surface (except on the cardinal area); and the 'minute granules' which were reputed to cover the whole shell are in fact the ends of the infillings of the punctae, which project slightly when the surface layers of the shell have been removed.

The large spines, non-lamellose shell, and relatively small boss for the cardinal process permit the rapid discrimination of this species. It is possible that the jugum is complete in some specimens, but I have not observed this in my material.

Spiriferellina cristata (Schlotheim)

Plate 59, figs. 1–9; Plate 60, fig. 3

Material. Lectotype (here chosen) B.-K. Sp. 33.1 collection of the Geologisch-Paläontologisches Institut und Museum, Berlin: from the Zechstein of Glücksbrunnen, Thüringen. The remainder of Schlotheim's syntypes are in the same institution, numbers B.-K. Sp. 33.2 to B.-K. Sp. 33.12. In addition 5 topotypes in the Sedgwick Museum and about 20 specimens from Pössneck, Thuringia, in the British Museum, have been examined.



TEXT-FIG. 5. Serial sections of a specimen of *Spiriferellina cristata* (Schlotheim). The intervals between sections 10 and 11, and 16 and 17, are 0·02 inch; the remainder are 0·01 inch. ×3. BB 20430, B.M.

Description of type specimens. Most of the specimens are in a poor state of preservation and many are fragmentary.

The shell is small, the largest having a maximum width of *c.* 14 mm. The pedicle umbo is rather high and pointed and curved over the cardinal area at its tip. Throughout ontogeny the cardinal extremities are well rounded, and hence the lateral slopes curve around on to a subdued, more or less rounded cardinal ridge. The plicae are high and subangular and usually number four on each side of the sinus, with an incipient fifth. In all specimens the sides of the sinus are steep and the floor flat, the junction between the two being quite angular. In the largest specimens the floor tends to be slightly domed

towards the front. The fold and sinus have the appearance of being of the same order of magnitude as the bounding plicae.

The cardinal area meets the hinge almost at right angles to the plane of the commissure, and its concavity is very slight except toward the umbo where it increases abruptly. There are traces of transverse striae on the area, but there are no signs of denticles or denticle grooves.

The brachial valve has a prominent little umbo and a strongly concave area. The fold is rather sharp with a rather rounded crest at the juvenile stage. No adult folds are preserved.

The surface lamellae are very variably arranged. On some juveniles they are rather

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EXPLANATION OF PLATE 58

All figures are of topotypes, and all $\times 2$.

Figs. 1–10. *Punctospirifer scabricosta* North. 1*a–e*, Ventral, dorsal, posterior, anterior, and lateral views, E 10405 S.M. 2*a–d*, Ventral, dorsal, posterior, and anterior views, E 10403 S.M. 3*a–e*, Ventral, dorsal, posterior, anterior, and lateral views, E 10404 S.M. 4*a–e*, Same, E 10402 S.M. 5*a–d*, Ventral, dorsal, posterior, and anterior views, JGG 1260 G.S.M. 6*a–d*, Ventral, posterior, anterior, and lateral views, E 10406 S.M. 7*a–b*, Interior of a brachial valve, and rubber mould of same. The blemish on the infilling of the socket on the right of the specimen is due to faulty casting. E 10422 S.M. 8*a–b*, Same, E 10421 S.M. 9, Interior of a brachial valve, E 10420 S.M. Note the differing forms of the cardinal process in these three specimens. 10, Prepared section of a complete specimen cut through the two umbones and down one dental lamella and adminicula. Note the small callus in the pedicle umbo, the ridges on the inner face of the dental lamella, the dental ridge, and the descending lamella of the spire, E 10407 S.M.

EXPLANATION OF PLATE 59

All figures $\times 2$.

Figs. 1–9. *Spiriferellina cristata* (Schlotheim). 1*a–c*, Dorsal, anterior, and posterior views of a syntype, B.K. Sp. 33.2 H.U.B. 2*a–e*, Ventral, dorsal, anterior, posterior, and lateral views, BB. 20432 B.M. 3*a–d*, Ventral, dorsal, anterior, and lateral views, BB. 20435 B.M. 4*a–d*, Ventral, dorsal, anterior, and posterior views, BB. 20434 B.M. 5*a–c*, Ventral, dorsal, and anterior views of a syntype, B.K. Sp. 33.3 H.U.B. 6*a–b*, Dorsal and anterior views, BB. 20433. 7*a–b*, Ventral and posterior views of the lectotype. 8, Internal view of a broken specimen showing the spires, BB. 20440 B.M. 9, Same showing spires, end of the ventral septum, and the incomplete jugum, BB. 20441 B.M. Specimens 2–4, 6, 8–9 from Pössneck.

Figs. 10–15. *Reticulariina spinosa* (Norwood and Pratten). 10*a–d*, Ventral, dorsal, anterior, and lateral views of a large specimen, BB. 7930 B.M. 11*a–e*, Ventral, dorsal, anterior, posterior, and lateral views, BB. 20436 B.M. Note the spines on the cardinal area of 11*d*. 12*a–d*, Ventral, dorsal, lateral, and posterior views, BB. 20437 B.M. 13*a–b*, Ventral and dorsal views, BB. 20439 B.M. 14, Interior of a brachial valve, E 16227 S.M. Note the sharp inflection of the inner edges of the crural plates. 15*a–c*, Ventral, dorsal, and posterior views, BB. 20438 B.M. Note the position of the ventral adminicula and the crural plates in 15*c*. All specimens from Chester, Illinois.

EXPLANATION OF PLATE 60

Figs. 1, 2. *Punctospirifer scabricosta* North. 1, Ventral view of E 10402 S.M. The cellular structure on the centre of the specimen is a bryozoan, $\times 7{\cdot}2$. 2, Part of the sinus of the holotype, $\times 8$.

Fig. 3. *Spiriferellina cristata* (Schlotheim). Ventral view of lectotype, $\times 7{\cdot}2$.

Figs. 4, 5. *Reticulariina spinosa* (Norwood and Pratten). 4, Part of the brachial valve of a specimen from Chester showing the spines and the ends of the infillings of the punctae, BB. 20437 B.M., $\times 7{\cdot}2$. 5, Ventral view of a specimen from Chester, showing the arrangement of the spines, E 16226 S.M., $\times 3{\cdot}2$.


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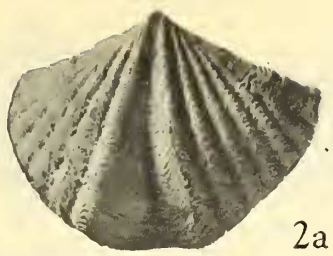
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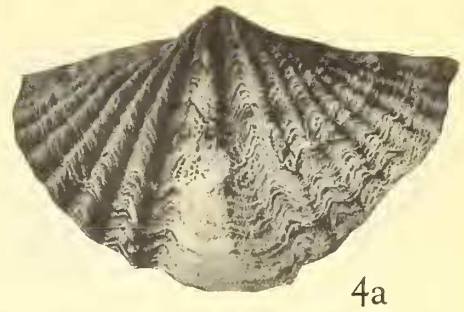
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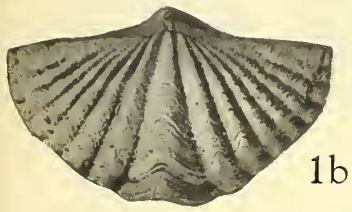
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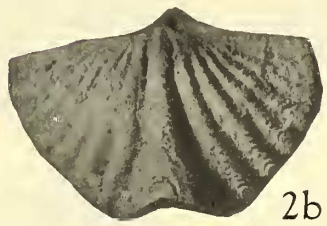
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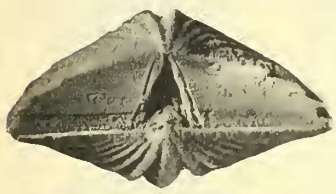
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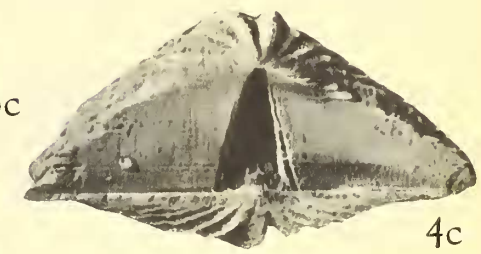
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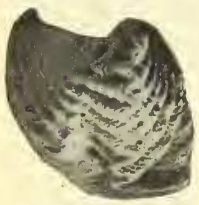
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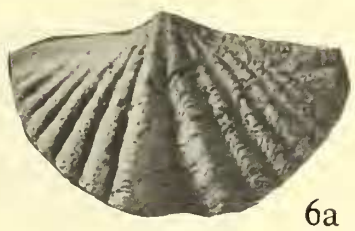
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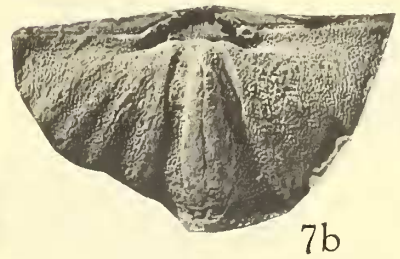
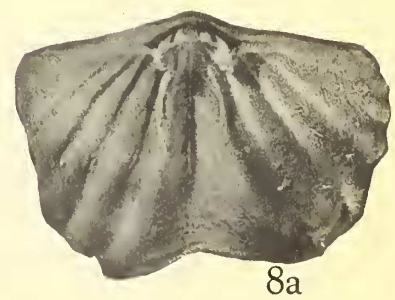
6b


7a


5b


6c

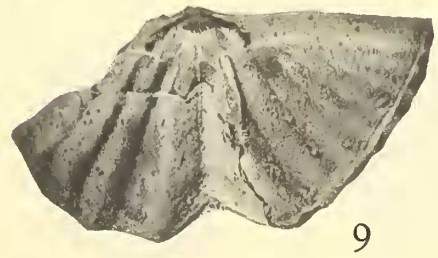

7b


8a


5c


6d

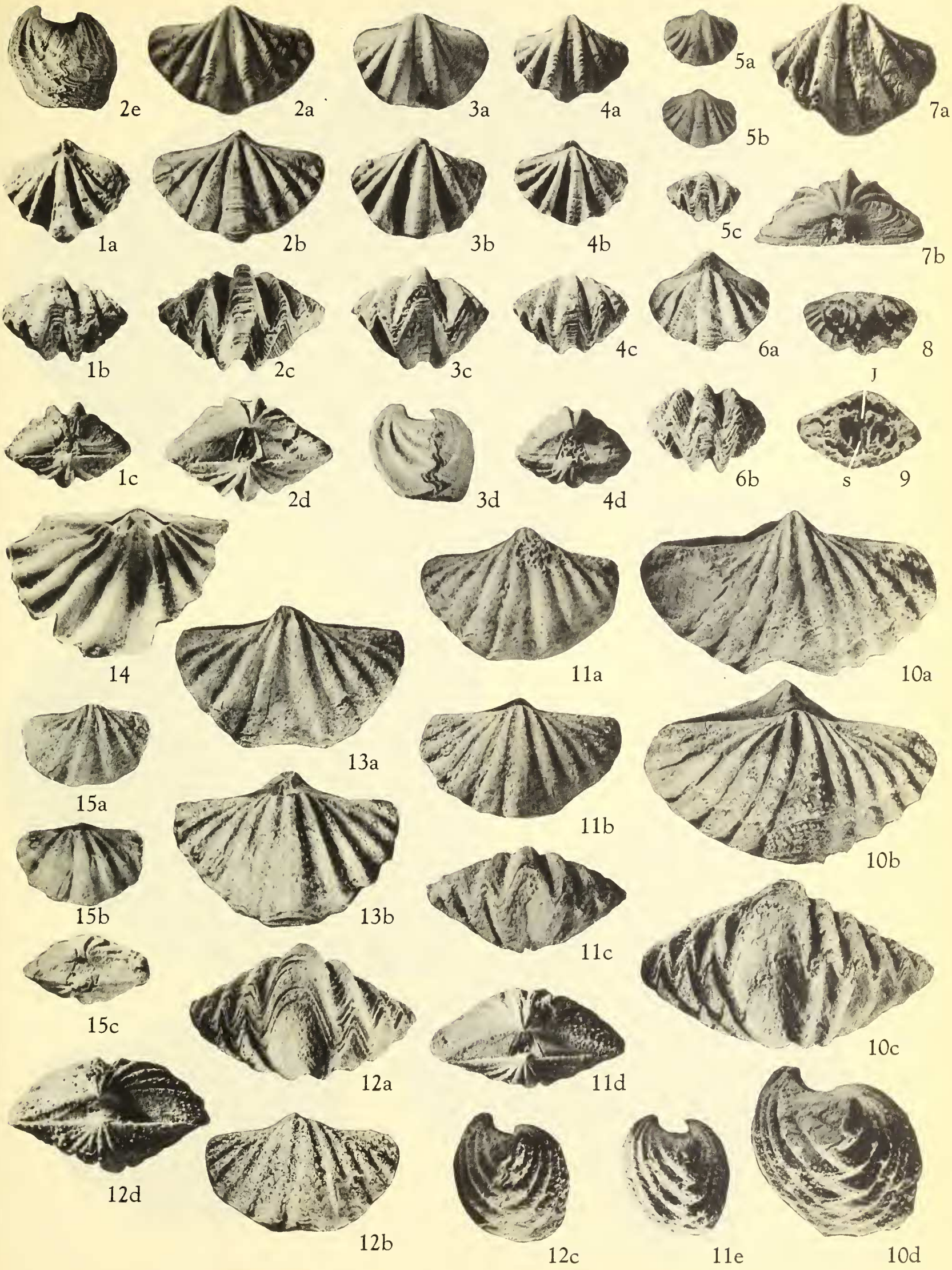

10


9


8b


5d

CAMPBELL, *Punctospirifer scabricosta*, all x2



CAMPBELL, *Spiriferellina* and *Reticulariina*